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Obedience and Overimitation in Domestic Dogs

Master's Thesis

Interdisciplinary Master's in Human Animal Interactions

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Abstract

Overimitation, the copying of functionally irrelevant actions, is a form of social learning important for the transmission of culture. Though long believed to be uniquely human, as it has not been found in any other primate species thus far, overimitation was shown in recent years to be performed by dogs. Domestic dogs overimitate their human caregivers, more so than strangers, in a task where irrelevant actions (touching wall-mounted dots) and a goal-directed action (opening a door to get food) are demonstrated. In this study, we used the same task to check whether dogs overimitate because of audience effects - if the dog is being watched (or not) by their caregiver. Audience effects are associated with dog obedience, where dogs are more likely to steal food if they are not being watched. But in children, an audience can facilitate affiliative overimitation since these social signals would need a receiver. To do this, we used the caregiver as a demonstrator, and two conditions of varying attentional state of the caregiver during the trials (watching the dog or facing the wall). Our results did not support obedience as the driving force for overimitation in dogs as we found no difference between conditions for the copying of the irrelevant action. However, dogs more accurately copied the goal-relevant action when being watched. This provides more evidence for the hypothesis that dogs overimitate for social affiliative reasons rather than obedience. The possibility that affiliation and obedience are linked for dogs' overimitation behaviour is discussed.

Zusammenfassung

Überimitation, das Kopieren von funktionell irrelevanten Handlungen, ist eine Form des sozialen Lernens, die für die Weitergabe von Kultur wichtig ist. Obwohl man lange Zeit glaubte, dass dies nur beim Menschen vorkommt, da es bisher bei keiner anderen Primatenart gefunden wurde, konnte in den letzten Jahren gezeigt werden, dass auch Hunde diese Fähigkeit besitzen. Haushunde ahmen ihre menschlichen Bezugspersonen bei einer Aufgabe, bei der irrelevante Handlungen (Berühren von an der Wand befestigten Punkten) und eine zielgerichtete Handlung (Öffnen einer Tür, um Futter zu bekommen) gezeigt werden, stärker nach als Fremde. In dieser Studie haben wir dieselbe Aufgabe verwendet, um zu überprüfen, ob Hunde aufgrund von Publikumseffekten übermäßig imitieren - wenn der Hund von seiner Bezugsperson beobachtet wird (oder nicht). Publikumseffekte werden mit dem Gehorsam von Hunden in Verbindung gebracht, die eher bereit sind, Futter zu stehlen, wenn sie nicht beobachtet werden. Bei Kindern kann ein Publikum jedoch die affiliative Überreizung erleichtern, da diese sozialen Signale einen Empfänger benötigen würden. Zu diesem Zweck verwendeten wir die Betreuungsperson als Demonstrator und zwei Bedingungen mit unterschiedlichem Aufmerksamkeitszustand der Betreuungsperson während der Versuche (Beobachtung des Hundes oder Blick auf die Wand). Unsere Ergebnisse sprechen nicht für Gehorsam als treibende Kraft für die Überimitation bei Hunden, da wir keinen Unterschied zwischen den Bedingungen für das Kopieren der irrelevanten Handlung fanden. Allerdings kopierten die Hunde die zielrelevante Handlung genauer, wenn sie beobachtet wurden. Dies ist ein weiterer Beleg für die Hypothese, dass Hunde aus Gründen der sozialen Zugehörigkeit und nicht aus Gehorsam überimitieren. Es wird die Möglichkeit erörtert, dass Zugehörigkeit und Gehorsam im Zusammenhang mit dem Nachahmungsverhalten von Hunden stehen.

Introduction

Social Learning

The modulation of learning by the social context has long been an area of great interest in the field of comparative cognition. As a behavioural and cognitive strategy, social learning is highly advantageous, allowing individuals to gather information from another about their environment without incurring the risks that come with trial and error. Considering its adaptive value, it is therefore unsurprising that social learning can be found not only in humans, but in a very wide range of animals. It allows individuals to learn about a wide range of topics such as food choice, location of resources, ways of communicating with conspecifics, hunting and defence strategies, problem solving, or mate seduction (Galef & Laland, 2005). To successfully transmit all of this, a few different types of social learning have been documented, although the classification of social learning mechanisms and categories are highly debated and ever changing. For this introduction, I will briefly discuss various social learning categories (Heyes, 1994; Van Schaik, 2010), which can be summarised as follows: social or response facilitation, enhancement, emulation and imitation. Perhaps the simplest form of social learning, facilitation is simply increased activity in an individual, due to another individual being nearby. Slightly more complex, local or stimulus enhancement is an increase in interest or motivation of an individual towards an object, due to a conspecific's actions in a certain location or upon said object. As for emulation and imitation, these are considered much more cognitively complex and require an individual to observe another's specific actions in order to learn by copying these new actions (imitation) or the goal of the action (emulation).

One unusual form of social learning, which has garnered more interest in recent years and is the topic of this thesis, is overimitation. First defined in Lyons et al. (2007), overimitation is the copying of causally irrelevant actions within a goal-directed action sequence. Although this might appear an unnecessary and even costly form of social learning, it is in truth a fundamental type of social learning for the transmission of culture (Legare & Nielsen, 2015; Tennie et al., 2009).

Indeed, social learning mechanisms involving the copying of another individual's behaviour play a very important role in the transmission of behavioural traditions and cultural practices (Heyes et al., 2009; Tennie et al., 2009; Whiten et al., 2009). As the subject of culture in non-human animals has been at the centre of many debates in the field of animal behaviour

and cognition, studying whether non-human animals are capable of copying their conspecifics' and heterospecifics' behaviour and, if so, to what extent, is of great importance. I will therefore now discuss imitation, overimitation and culture. If we consider culture to be stable behavioural variants unique to a population and not solely a product of their natural habitat (Whiten et al., 1999), it is perhaps unsurprising that imitation and overimitation would play such important roles for cultural transmission. Indeed, as Nielsen and Tomaselli (2010) explain, when talking about cultural practices the details of a process are much more telling than the end goal of this process, as it is those which vary across populations, making for different traditions. This is precisely what high fidelity copying entails. Moreover, not all aspects of cultural practices are goal oriented or goal-relevant, specifically in humans where social norms can sometimes be rather arbitrary. As such, imitation and overimitation serve as efficient ways to pass on cultural information to the next generation (Nielsen, 2012). This vertical cultural-transmission process is especially true for cumulative culture, that is behavioural variants which accumulate modifications and improvements over generations, something which is still believed to be a uniquely human capacity, in great part due to our capacity for high-fidelity copying and overimitation (Legare & Nielsen, 2015; Tennie et al., 2009).

Overimitation in Humans

Despite overimitation's apparent lack of value, it is in fact a very important social learning mechanism for the transmission of culture, as previously outlined. As such, it has been widely documented in humans. In Lyons et al.'s (2007) study, children witnessed a demonstration of a container being opened to reveal a toy, with the demonstration containing inefficient actions such as tapping on the box with a feather before opening it. Despite a prior training phase in which the causal relevance of each action was made clear to the subjects, a significant number of children still overimitated during the test phase, that is they performed the irrelevant actions as well as the relevant ones needed to reach the goal. Additionally, when the experiment was repeated, but overimitation was made even less appealing by telling the subjects that the test was over and therefore removing any social pressures, as well as adding a time constraint, children kept overimitating. Furthermore, overimitation rates remained high even when subjects were explicitly told to ignore unnecessary actions. Considering these results, the authors argued that overimitation was motivated by causal confusion, that children do not understand the irrelevant actions to be unnecessary but as

causally relevant and needed in order to achieve the goal. This is known as the Automatic Causal Encoding (ACE) hypothesis (Lyons et al., 2007), an explanation which remains highly debated as children have been known to overimitate at similarly high levels whether or not the goal-container is transparent or opaque and the causal relevance of actions therefore clear or not (Horner & Whiten, 2005; McGuigan et al., 2007).

However, there are other possible motivations behind overimitation in humans. The first alternative to causal confusion is normative compliance or normative learning. Indeed, in clear opposition to Lyons et al. (2007), Kenward et al. (2010) argued that children understood actions irrelevant to the goal as necessary in a normative rather than causal manner. In their experiment, children copied actions irrelevant to the goal but generally did not do so when the irrelevant actions had been performed by the experimenter already, in the context of the experimenter and child operating the apparatus together. Moreover, the children were asked whether the goal could be obtained without performing the causally relevant or irrelevant action, and the majority answered that the goal was unobtainable without performing the relevant action but said they did not think the irrelevant action was needed or expressed that they did not know. As such, the authors interpreted that children did not encode the irrelevant actions as causally relevant but that they believe the irrelevant action to be normative. This rapid norm acquisition in a demonstrative context is common for human children who learn from their caregivers what social norms to follow, by copying their behaviour. Similarly, both Kenward (2012) and Keupp et al. (2013) argued for the normative explanation by showing, in their respective experiments, that not only children overimitated, but they also protested when a third-party performed the action sequence without the goal irrelevant action. The authors interpreted protest as an indication of children understanding that the causally irrelevant action was a norm to be followed within the bigger goal-oriented action sequence.

The second alternative to causal confusion and the third potential explanation for overimitation is social affiliation. Indeed, considering the social context in which overimitation is displayed, children copying adults' behaviour, there is a possibility that children are copying the demonstrators' inefficient actions in an attempt to affiliate with them, to get closer to them or please them. Social affiliation as a potential motivator for demonstrator copying was for example demonstrated by Nielsen and colleagues in their 2008 paper. In Nielsen et al's (2008) study, children were more likely to copy the model's actions when the model was socially responsive rather than unresponsive. Over & Carpenter (2012) further developed this idea and, similarly, Nielsen and Blank (2011) found that children were less likely to overimitate if the adult model left the room when they were free to interact with the

apparatus. Furthermore, Vivanti and colleagues made a significant contribution to this hypothesis by showing convincing evidence for it in their 2017 paper. In their study, children with either Autism Spectrum Disorder (ASD) or Williams syndrome (WS) were shown video demonstrations of containers being opened to reveal a desired toy, wherein one action was causally inefficient. Results showed that children with ASD were much less likely to copy the causally irrelevant action than children with WS. Considering the fact that a significant component of ASD is reduced social motivation and that the opposite is true for WS, the far lesser propensity of children with ASD to overimitate compared to children with WS was interpreted by the authors as an argument in favour of the social affiliation hypothesis. Although the authors did not discuss the possibility of normative motivation for overimitation, which could come into play considering ASD is also often defined by difficulty learning or following norms, their study does serve as an argument against causal confusion as a reason for overimitation.

In addition to why humans overimitate, an important as well as fascinating question is which humans overimitate. There is evidence supporting variation across ages and cultures for overimitation. In children, it appears that overimitation begins occurring early on, increases with age (McGuigan et al., 2007; McGuigan & Whiten, 2009) and carries into adulthood (Flynn & Smith, 2012), with adults being even more faithful copiers than children (McGuigan et al., 2011). In addition to occurring in various age groups, overimitation is seemingly also not restricted to a single cultural background, as it has been found in people of non-Western cultures (Nielsen & Tomaselli, 2010; Nielsen et al., 2014; Stengelin et al. 2019). Having established the importance, scope and possible motivations for overimitation in humans, I will now discuss this phenomenon in non-human animals.

Overimitation in Canines

Until recently, overimitation was considered to be a uniquely human phenomenon, as research on primates has remained disappointing. Indeed, chimpanzees (*Pan troglodytes*) have been found to employ emulation as opposed to overimitation (Horner & Whiten, 2005), orangutans (*Pongo pygmaeus*) have also failed to show overimitation (Nielsen & Susianto, 2011), and bonobos tested for overimitation have provided similarly negative results (Clay & Tennie, 2018). Considering our failure to find overimitation in our closest living relatives, it is no surprise that this social learning mechanism was believed to be another unique feat of our species for so long.

However, pet dogs (Canis familiaris) make very good candidates for overimitation. Despite being much further removed from humans than primates, phylogenetically speaking, companion dogs are fully integrated into human society and therefore have the advantage of social closeness. As "man's best friend" and arguably our species's closest animal companion, dogs show incredible communicative and cognitive skills. In the course of their extensive domestication history, they have been selected for various tasks and made into the perfect working and social partner for humans (Gacsi et al., 2009; Galibert et al., 2011; Miklosi et al., 2003). Dogs are excellent communicators, attentive to us, and able to read our cues such as pointing or gazing much better than chimpanzees or socialised wolves (Canis lupus) (Hare & Tomasello, 2005; Miklosi et al., 2003; Soproni et al. 2001). Moreover, not only can dogs read their conspecifics' emotions, they are also able to recognise human emotions (Albuquerque et al., 2016; Müller et al., 2015). Lastly, what makes them potential overimitators is their ability to copy other dogs and humans. Indeed, Range and colleagues (2007) showed that dogs were able to copy a conspecific model's actions and to adapt this copying to the context in which the demonstration took place: they copied the non-preferred way of reaching a goal (pawing instead of mouthing) if the model performed this action instead of the available preferred one, but did not perform the non-preferred action if the model demonstrated it while the preferred action was unavailable (pawing because the model had a ball in their mouth). As such, dogs are capable of copying selectively their conspecifics' actions as well as copy human demonstrated actions in do-as-I-do tasks (Huber et al., 2009; Topal et al., 2006). That is, dogs trained to copy certain actions could then, to some extent, generalise this copying to novel actions when instructed to do so.

Considering all of these findings about dogs' cognitive abilities, it perhaps comes as no surprise that dogs were indeed found to overimitate. In the first study to explore canine overimitation, Johnston and colleagues (2017) used a similar apparatus to the ones used in studies of human overimitation to compare overimitation in domestic dogs and dingoes (*Canis dingo*), a comparison of interest considering dingoes are wild relatives of dogs and an intermediate between domestic dogs and wolves. In this study, both dogs and dingoes were shown how to open a box containing a food reward, the demonstration containing an irrelevant action (moving a stick-shaped lever protruding from the side of the box) and a relevant action (opening the lid to get to the treat). Both dogs and dingoes copied both the irrelevant and relevant action, with dogs copying the irrelevant action more than dingoes overall. However, because the subjects' tendency to copy the irrelevant action decreased over the four trials, the authors argued that these results were proof against overimitation in

canids, on the grounds that they interpreted this performance as the subjects progressively learning the causal irrelevance of the lever and choosing to therefore stop using it. Despite the authors' interpretation however, it could be argued that their results show overimitation as the majority of dogs did use the irrelevant lever in their first trial and still half of the overall subjects copied the irrelevant action in their fourth trial. Moreover, the use of a box and toy lever could be questioned for canids, as the causal relevance of the actions could have been less transparent than assumed and the toy could have been rewarding on its own. To ensure that these issues do not come into play, an overimitation task better suited for dogs could have the irrelevant action be spatially separate from the relevant action leading to the reward as well as choose an irrelevant action holding no inherent appeal to the dog. This would increase clarity of the causal relevance of each action and allow for stronger investigation of overimitation.

In such a novel overimitation task, dogs showed copying of human demonstrators' causally irrelevant actions (Huber et al., 2018). The whole demonstration consisted of the dog's caregiver getting on their hands and knees, in a dog-like manner, and performing the causally irrelevant action of touching a blue then a yellow dot (mounted on the wall) with their nose. The caregiver then performs the causally relevant action of pushing a food chamber door open with their nose to reveal to the dog a food reward. In this first study, dog subjects were divided in four groups and saw either only the relevant, irrelevant actions or both actions in either order (irrelevant followed by relevant or the opposite). The authors found that dogs who had only seen one of the actions did not perform the other and that some of the dogs having seen both relevant and irrelevant actions showed overimitation. In a follow-up study (Huber et al., 2020), the same task was used with an unfamiliar human performing the demonstration. This resulted in much lower overimitation rates, suggesting that dogs were more likely to copy their caregivers' rather than strangers' functionally irrelevant actions. These studies would suggest that dogs, as might be the case in humans, overimitate for socio-affiliative reasons: they copy seemingly useless actions to affiliate with their caregivers, to get closer to them or as a kind of social game. To further test this hypothesis, Huber and colleagues performed a third overimitation study (2022) in which they performed the same task but added a relationship test to see whether the quality of the relationship between the dog and their caregiver correlated with overimitation rates. Although they could not confirm this to be the case - possibly because of a low sample size or low variance in the human-dog relationships – they did show that dogs with the highest overimitation scores showed more referential and affiliative behaviours towards their

caregivers. The fourth overimitation study conducted at the Clever Dog Lab to this date was done by Mackie & Huber (2023), wherein they tested whether dogs' overimitation of their caregivers could be modulated by priming. To do so, the same overimitation task as previous studies was used, but there were three priming conditions. The conditions consisted of no prime before the overimitation task, an attention prime and an attachment prime. The attention prime consisted of the subjects playing a cup game where food was hidden under one of three cups and the dog was made to choose a cup, after which they performed the overimitation task as usual. The attachment prime performed before the overimitation task was that of the Threatening Stranger (Vas et al., 2005), in which a masked stranger approached the dog-caregiver pair and the dog's reaction is analysed to assess their relationship to their caregiver. The results of their study found no difference in overimitation between the three conditions, but priming versus no priming seemed to have a small numerical difference. Notably, dogs often copied the irrelevant actions after already receiving their food reward, pointing again to social (rather than goal-orientated) motivations. Despite the findings of these previous overimitation studies all pointing in the direction of dogs overimitating to affiliate with their caregivers, there remains an alternative explanation to be explored, that of obedience.

As previously explained, dogs have been selected to be our social and working companions, thus potentially to be very eager to please and obey humans. Additionally, obedience could perhaps explain why dogs overimitate their caregivers more readily than strangers, considering caregivers are generally the ones who train them, potentially from puppyhood, and who they are expected to obey the most, or at least more than a stranger. As such, the subject of my thesis is to test whether obedience influences a dog's propensity to overimitate. As dogs could view the overimitation task as a social game and an opportunity to affiliate to their caregiver, so could they view it as a kind of training session, a way to please them by copying them faithfully, or think that faithful copying is what is expected of them.

In order to explore this question of the role of obedience in pet dog overimitation, we must define and detail what is meant by obedience. Obedience in pet dogs is to be understood here as a dog's willingness to obey their caregiver's commands and rules. It may be modulated by each dog's personality and breed as well as their training experience. From previous studies, we know that dogs' compliance to known commands varies based on the context such as handler position and distance (Fukuzawa et al., 2005) and increases with obedience training (Clark & Boyer, 1993; Kobelt et al., 2003). In addition, it has been shown

that behavioural issues in pet dogs such as aggression, overexcitability or separation problems decrease with obedience training (Bennett & Rohlf, 2007; Clark & Boyer, 1993; Jagoe & Serpell, 1996; Voith et al., 1992) and that obedience training improves the human-dog relationship (Clark & Boyer; 1993). Lastly, some studies have focused on the effect of training on dog behaviour in cognitive tasks, finding that the type of training received affected the response of the dog in a food acquisition task. For example, dogs trained in search and rescue showed less human-directed gazing than dogs trained in agility (Marshall-Pescini et al., 2009). And dogs with extensive training experience were more successful in a problem solving task than dogs with no or basic training (Marshall-Pescini et al., 2008 and 2016).

I therefore hypothesise that the propensity of dogs to overimitate is related to their level of obedience. In order to test this hypothesis, I used variation of attentional states to modulate obedience, as it is known that dogs are sensitive to humans' attentional states and that they grow more likely to disobey as their caregivers' attentiveness decreases (Call et al., 2003; Schwab & Huber, 2006; Viranyi et al., 2004). Additionally, it has been shown that the attention of the demonstrator affects overimitation in humans as children's propensity to overimitate decreases with the demonstrator's attentiveness, though in the case of children, this was interpreted as an opportunity to affiliate with the demonstrator that decreased with the demonstrator's attentiveness (Marsh et al., 2019; Stengelin et al., 2019). Similarly to Marsh et al. (2019), my initial experimental design consisted of the same overimitation task performed in three conditions of varying attentiveness: after their demonstration, during the dog's imitation test, the caregiver watched, turned their back or left the room. In line with our hypothesis, I predicted that dogs in the most attentive condition (caregiver watching) would be the most inclined to obey and therefore overimitate the most whereas dogs in the least attentive condition (caregiver leaving) would be the most likely to disobey and therefore overimitate the least. As we had to remove the condition where the caregiver left the room due to ethical and methodical concerns as several dogs exhibited signs of separation distress (Flannigan & Dodman, 2001; Mendl et al., 2010; Sherman, 2008), the second prediction applies to the initial medium condition wherein the caregiver turns their back to the dog.

Materials and Methods

Ethics statement

The study was discussed and approved by the institutional ethics and animal welfare committee in accordance with GSP guidelines and national legislation (approval number: ETK-173/10/2022). Written consent by the dog caregivers was obtained prior to the data collection.

Subjects

The study took place at the Clever Dog Lab (CDL) of the Messerli Research Institute, at the Veterinary University Vienna, where caregivers volunteer to come with their dogs to participate in behavioural and cognitive research. Participants were recruited from the CDL database containing caregivers having already participated in studies or having expressed their willingness to, on social media and in person such as at the dog park. The requirements for participation were for the dog to be between one and twelve years old, tall enough to reach our apparatus door (above 30 centimetres), food motivated, and naive to the overimitation task (to avoid learning effects).

We aimed at having 60 subjects, 30 per condition. Indeed, I tested 78 dogs overall and ended up with 63 subjects after exclusions, 33 in condition 1 and 30 in condition 2. Reasons for exclusions (eleven dogs) were; technical issues, caregiver or experimenter error, dogs in the removed condition 3, dogs used for piloting (four dogs). The first 15 dogs were randomly assigned to their conditions and the rest were assigned to make sure our conditions were balanced in terms of age, sex and breed. As such, I ended up with 16 females and 17 males in condition 1, 15 females and 15 males in condition 2. Breeds represented varied greatly but no breed was overrepresented, mixed breeds represented the highest number of subjects among all the breeds. A complete list of participants can be found in the Supplementary Materials (S1).

Procedure

Testing was done in a single half-hour session consisting of a one-minute exploration phase where the dog was free to explore the room off-leash, with the caregiver and experimenter present, an obedience test, an attention warm-up and finally the overimitation task with four trials (Figure 1). The obedience test was verbally explained to the caregiver while the attention warm-up and the overimitation task were instructed using demonstration videos. The entire session took place in a testing room (6.0×3.3 m), equipped with three cameras to record the testing.

Obedience test

An obedience test was designed and added during testing to enrich the study, therefore not all dogs took part in the test but out of the 63 non-excluded subjects, obedience data was obtained from 60 dogs. The test lasted one minute, during which the experimenter sat in a chair. The caregivers were asked to instruct their dog to perform five behaviours: sitting next to the experimenter, staying in the sit for 20 seconds while the caregiver went 2 metres away to kneel on a blanket, going back to the caregiver when called, going back to the experimenter while the caregiver stayed on the blanket and sitting again, away from their caregiver. If the dog could not perform all the behaviours in the given time, the test still ended at the minute mark. No food reward was used during the test, for all the dogs. Obedience scores were out of five, with one point for each successful command.

Attention warm-up

Once the obedience test was done, the attention warm-up was performed, to stimulate the dogs' attention and get them focused on the caregiver for the overimitation task. The attention warm-up used was the so-called "cup game" in which a piece of food is hidden under one of three cups and the dog is expected to choose a cup by sniffing or touching. Since this game was not meant to be difficult, the baiting was done in full view of the dog and there was no shuffling of the cups. During the game, the dog was held by the experimenter during the baiting and free once they were expected to choose a cup. The reward used for most of the dogs was a piece of kibble, but if dogs could not eat this, caregivers were asked to bring their own treats. We performed six rounds of the game, with the baited cup being as follows: middle, middle, left, right, middle.

Overimitation task

The overimitation task used was a replication of Huber et al. (2018, 2020, 2022) during which the dogs' primary caregiver demonstrated first the functionally irrelevant action (Image 1) and then the goal-directed action (Image 2), both in a dog-like manner. For the relevant action, a white wooden wall (150×100 cm) with a central cut-out covered by a sliding door (10×9 cm, 50 cm above the ground) was installed (Image 2). The door could be opened in both directions (with a wooden handle) and behind it was a food chamber. For the irrelevant action, a white laminated poster (172×106 cm) was placed on the same wall as the sliding door, at a distance of 130 cm. Two white, A4-sized sheets of paper with printed colour dots (9 cm in diagonal; one blue and one yellow) were taped to the poster (50 cm above the floor) (Image 1). To ensure scent cues from previously tested dogs did not influence dogs being tested, the poster and the white wooden wall, including the sliding door, were cleaned between sessions with alcohol. The colour dots were newly printed for every dog.

The test was conducted as follows: the caregiver started on the left of the experimenter, walked over to the wall with the dots, got on her/his hands and knees, touched the blue dot with her/his nose, walked to the yellow dot, touched it with her/his nose (Image 3), walked to the wall with the food chamber, pushed the sliding door open towards the left with her/his nose (Image 4), took the food reward out, showed it to the dog, put it back and finally closed the door before walking back to the starting position. Before performing each of the actions, caregivers were instructed to look at the dog to ensure the dog was paying attention and to call out to them if not. During the entirety of the demonstration, the experimenter was sitting and holding the dog. The food reward used was predominantly a piece of sausage but if the dog could not eat this, caregivers were instructed to bring their own high-value treats.



Figure 1: First target of the overimitation task, the dots to be touched for the irrelevant action.



Figure 2: Second target of the overimitation task, the food chamber door to be pushed open for the relevant action.

Once the caregiver was back in her/his starting position, the dog was released and free to do as it pleased in the room, for one minute (Images 5, 6). During this minute, I, the experimenter, stayed seated and stared at the wall in front of me until the timer went off, signalling the end of a trial. Four trials were performed, each preceded by a caregiver demonstration. If the dog did not move upon being let go, the caregiver was instructed to release her/his dog verbally but to avoid commanding them to do anything such as "search". Importantly, the attentional level of the caregiver during the trials varied based on the condition the dog was assigned to. Each dog only experienced one condition. For condition 1 or the attentive condition, the caregiver had her/his back to the wall, faced the testing room and were instructed to watch her/his dog during the entirety of the trial, eye contact was allowed but the handler was asked to keep her/his reactions, verbal or otherwise, to a minimum. For condition 2 or the inattentive condition, the handler, upon completing the demonstration, would face the wall, effectively having her/his back to the room and their dog. They were asked to stare at the wall until the timer went off and to avoid reacting to their dog, should they vocalise or jump on them. A third condition was initially included in the study, where the caregiver left the room after performing the demonstration and the dog was left with only the experimenter during the trial. This condition was however removed as it proved too stressful for some dogs, causing them to remain at the testing room door and not engage in the task.

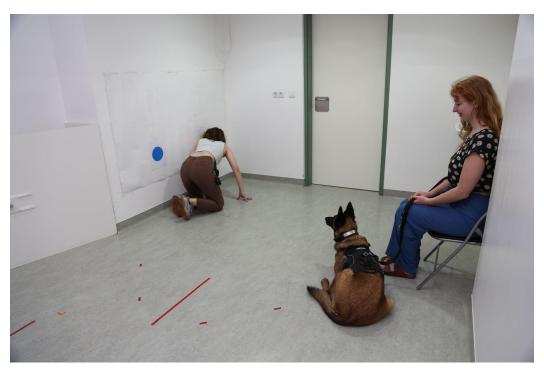


Figure 3: A caregiver demonstrating the irrelevant action by touching the yellow dot with her nose while on all-fours, with the experimenter holding the dog and the dog watching the demonstration.



Figure 4: A caregiver demonstrating the relevant action by pushing open the food chamber door with her nose while on all-fours, with the experimenter holding the dog and the dog watching the demonstration.

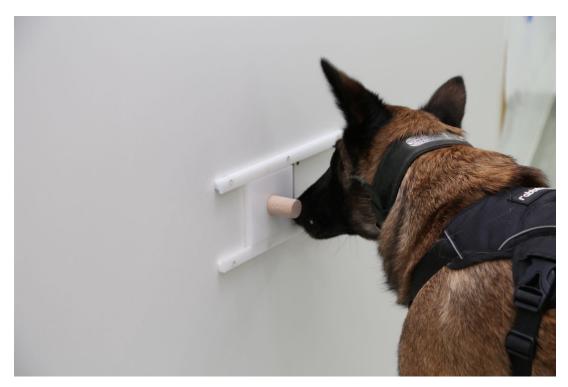


Figure 5: Example of a dog copying the relevant action by pushing the food chamber door open with its nose.

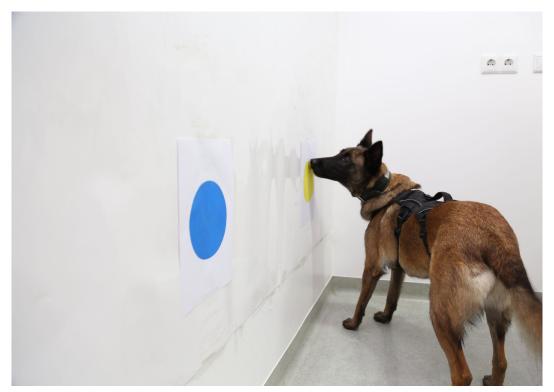


Figure 6: Example of a dog copying the irrelevant action by touching the yellow dot with its nose.

Data analysis

Video scoring

All videos of the testing were uploaded to the in-house Loopy server and scoring was done on the same platform before all the data was gathered in an Excel sheet for statistical analysis. The exploration phase was not scored as it was only for habituation and neither was the cup game as it merely served as an attention prime following Mackie & Huber's (2023) findings that overimitation was higher when dogs received either an attention or a relationship prime prior to the overimitation task, as compared to no prime. The obedience test was scored by giving each dog one point per successful action, leading to a maximum score of five. As for the overimitation task, copying accuracy scores were created for both the relevant and irrelevant actions, as detailed below (Table 1).

Table 1: Description of the copying accuracy scores of the Irrelevant and Relevant actions, used for coding the videos.

Copying Accuracy	Irrelevant Action	Relevant Action
0	No approach of the wall with dots	No approach of the wall with food chamber
1	Approach of the wall/dog walked directly in front of wall/smelled in front of it	Approach of the wall/dog walked directly in front of wall/smelled in front of it
2	Touching of one of the dots with nose	Touching of apparatus with nose
3	Touching of both dots with nose, in wrong order (yellow, blue)	Pushing open of door with nose, in wrong direction (towards right)
4	Touching of both dots with nose, in right order (blue, yellow)	Pushing open of door with door, in right direction (towards left)

Statistics

The data was analysed using the software RStudio. To examine whether the attentional state of caregivers affected the dogs' performance during the overimitation task, I performed a Mann-Whitney-U test to compare the copying accuracy of the irrelevant action between the two conditions and the same test to compare the copying accuracy of the relevant action between conditions.

Furthermore, to estimate the effect that attentional state has on performance during the overimitation task we fitted an ordinal (i.e., cumulative logit link) mixed model (Agresti, 2000). We build two models, one with the copying accuracy score of the irrelevant action (OI_score) and one using the copying accuracy score of the relevant action (REL_score) as response variables. Both models were identical and included *condition* as a test predictor of interest, and *trial number, age squared* and *sex* as control predictors. We also included *subject* as random intercept effect to account for repeated measurements of the same individuals and *trial* within *subject* as a random slope effect (Barr et al., 2013; Schielzeth & Forstmeier, 2009). The obedience score was not included in the model as it proved difficult to accurately score, given the variation of dog behaviours during the obedience test. This measure would have required us to subset the data. We fitted the model in R (Version 4.2.0) (R core team, 2022) using the clmm function of the package ordinal (Version 2020.8-22). Prior to fitting the model we z.transformed the covariates trial number and age, to ease model convergence and achieve easier interpretable model coefficients (Schielzeth, 2010). The full ordinal mixed models are shown below.

OI_Score ~ Condition + z.trial + z.age + I(z.age^2) + sex + (1 + z.trial | subject) REL_Score ~ Condition + z.trial + z.age + I(z.age^2) + sex + (1 + z.trial | subject)

We verified the absence of collinearity by calculating the Variance Inflation Factor (VIF) for a corresponding linear mixed model using the R package "car" version 3.0-12 (Fox & Weisberg, 2019). This revealed that collinearity was not an issue (max VIFREL_score: 1.21; max VIFOI_score: 1.16). After fitting the model we confirmed that model assumptions of proportional odds were not violated by dichotomizing the copying behaviour as at least 1; at least 2; at least 3; and at least 4, fitting logistic models with the obtained response variables, and inspecting the model estimates. These varied only little, suggesting the assumption was not strongly violated. We assessed model stability with respect to the model

estimates by comparing the estimates from the model including all data with estimates obtained from models in which individuals were excluded one at a time (Nieuwenhuis et al., 2012). This revealed that the model is of good stability. We determined the significance of individual predictors by dropping them from the full model, one at a time, and comparing the resulting model with the full model. For model comparisons we used a likelihood ratio test (Dobson, 2002). We calculated 95% confidence intervals for the model estimates and fitted values by applying the function 'bootMer' of the package 'Ime4', applying 1,000 parametric bootstraps.

Results

Overview

Out of the 63 subjects, 23 dogs copied the irrelevant action by touching at least one of the dots in at least one trial, which I considered as a weak case of overimitation. Out of the 23 "modest overimitators", 3 dogs obtained the highest score by touching both dots in the correct order, making them "perfect overimitators". Overimitation (at least in the weak manner as described above) took place in 34 trials (Table 2), 19 of those being performed by dogs in the attentive condition and 15 by dogs in the inattentive condition. As for the relevant action, 33 managed to open the door and consumed the food reward in at least one trial.

	Copying accuracy	Trials total	Attentive condition	Inattentive condition
	0	102	56	46
	1	115	57	58
Irrelevant action	2	30	18	12
	3	1	0	1
	4	3	1	2
	0	27	6	21
Relevant action	1	45	20	25

<u>Table 2</u>: Frequencies of copying actions divided according to accuracy score, for the relevant and irrelevant action, in the attentive and inattentive condition, all of the four trials compiled.

2	54	33	21
3	31	15	16
4	78	46	32

In the attentive condition where the caregiver watched the dog, 36% of dogs (12/33) overimitated by touching at least one dot in at least one trial (Figure 1) and 58% (19/33) opened the door and ate the reward. In the inattentive condition where the caregiver turned their back on the dog and faced the wall, 37% of dogs (11/30) overimitated and 47% (14/30) ate the food reward.

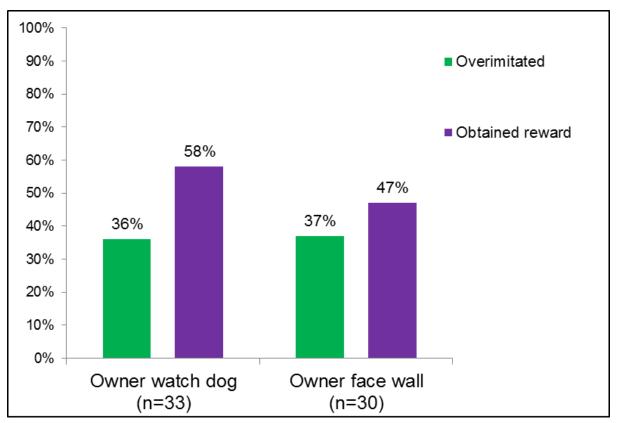


Figure 7: Percentages of subjects having performed the relevant and irrelevant action in at least one trial (scoring 2+ for the irrelevant-action score and 3+ for the relevant-action score), for both the attentive and inattentive condition.

In the 23 overimitators, 7 dogs overimitated in more than one trial. Out of the 23 overimitators (Table 3), 10 were male and 13 female. Ages varied greatly between 1 to 9 years and so did breeds, with mixed breeds being overrepresented (as in the overall sample).

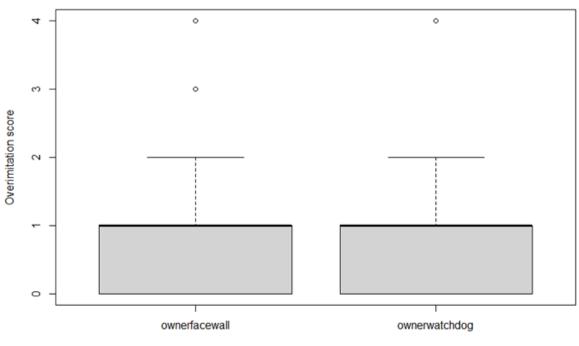
Name	Age	Breed	Sex
Milo7*	3	Australian Shepherd	М
Boo2	9	Міх	F
Yuki7	3	Mix	F
Jack7	1	Australian Shepherd	М
Nikita4	4	Australian Shepherd	F
Maze	1	Mix	F
Pisco*	1	Parson Jack Russell Terrier	М
Siri*	6	Border Collie	F
Kalea	2	Labrador Retriever	F
Hero	1	Whippet	М
Mazekeen	4	Kleiner Münsterländer	F
Loki7	1	Mix	М
Arthur3	8	Rhodesian Ridgeback	М
Gandalf	3	Andalusian Hound	М
Nala15	1	Mix	F
Daisy5	2	Golden Retriever	F
Nala16	1	Golden Retriever	F
Resi2	1	Magyar Vizsla	F
Flee	4	Siberian Husky	М

Table 3: List of all the dogs having copied the irrelevant action at least once, detailing their name, age, breed and sex (names marked with an * are "perfect overimitators").

Tofu	1	Cocker Spaniel	М
Terence	4	Welsh Corgi Pembroke	М
Lina3	7	Міх	F
Ella3	1	Міх	F

Effect of condition on overimitation

Mean copying accuracy of the dot touching action was 0.73 in the attentive condition and 0.78 in the inattentive condition (Figure 2). The Mann-Whitney-U test revealed the difference of mean copying accuracy of the irrelevant action between conditions to be non-significant (p-value=0.71).



Comparison of overimitation per condition

Owner attentional state

Figure 8: Boxplot of the copying accuracies of the irrelevant action in the attentive ("ownerwatchdog") and inattentive ("ownerfacewall") condition.

The full-null model comparison for the copying accuracy of irrelevant actions was non-significant (χ^2 =0.066, df=1, p=0.797), meaning that our test predictor had no effect on our response variable, caregiver attentional state did not affect irrelevant action copying. The model revealed no significant effect of condition, age, age squared or sex on our response variable but a significant effect of trial (p<0.05) (Table 4). The copying accuracy of the irrelevant action in our subjects did not differ significantly between attentional state conditions (Figure 3).

Table 4: Results of the ordinal mixed model for the copying accuracy of the irrelevant action (N=251), with the inattentive condition (*ownerfacewall*) being the reference category for *condition* and female the reference category for *sex*. 0|1 represents the comparison between scores 0 and 1 of the irrelevant action copying, as do 1|2, 2|3 and 3|4.

Effect	Estimate	Std. Error	z-value	P-value
0 1	-0.5028	0.4317	-1.1646	0.2442
1 2	2.2269	0.4686	4.7524	0.0000
2 3	4.6822	0.6843	6.8425	0.0000
3 4	4.9820	0.7435	6.7004	0.0000
Attentive Condition	0.1037	0.4030	0.2572	0.797
z.trial	-0.3216	0.1333	-2.4127	0.0158
z.age	-0.1903	0.2689	-0.7076	0.4792
l(z.age^2)	-0.0458	0.1673	-0.2739	0.7842
sexM	-0.0949	0.3833	-0.2475	0.8045

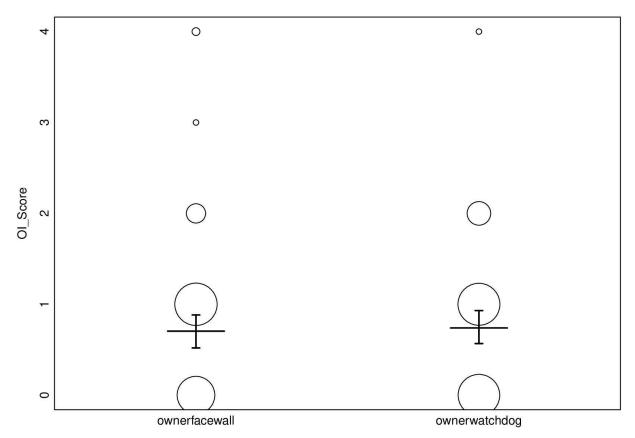
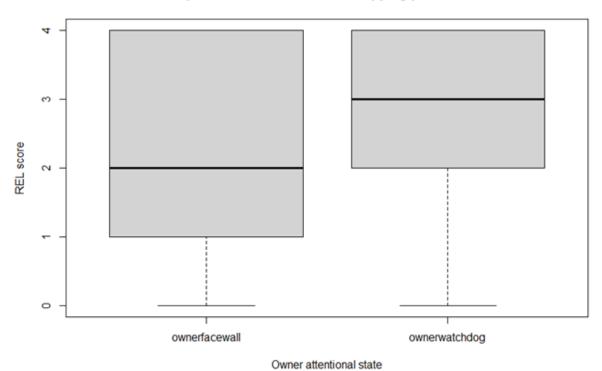


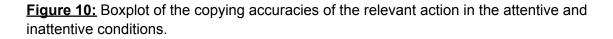
Figure 9: Irrelevant action copying scores depending on the caregiver's attentional state, circles represent the number of individuals and lines represent the average score.

Effect of condition on relevant action copying

Mean copying accuracy of the door opening action was 2.63 in the attentive condition and 2.11 in the inattentive condition (Figure 3). The Mann-Whitney-U test revealed the difference of mean copying accuracy of the relevant action between conditions to be significant (p-value<0.05).



Comparison of relevant action copying per condition



The full-null model comparison for the copying accuracy of relevant actions was significant (χ^2 =4.575, df=1, p<0.05), meaning that our test predictor had an effect on our response variable, caregiver attentional state affected relevant action copying. The model revealed a significant effect of condition, age squared (p<0.05) and trial (p<0.05) on our response variable but no significant effect of age and sex (Table 5). The copying accuracy of the relevant action in our subjects differed significantly between attentional state conditions (Figure 5). Dogs in the attentive condition had significantly higher copying accuracy scores than dogs in the inattentive condition (estimate=1.9276, p<0.0352).

Table 5: Results of the ordinal mixed model for the copying accuracy of the relevant action (N=235), with the inattentive condition (*ownerfacewall*) being the reference category for *condition* and female the reference category for *sex*. 0|1 represents the comparison between scores 0 and 1 of the relevant action copying, as do 1|2, 2|3 and 3|4.

Effect	Estimate	Std. Error	z-value	P-value
0 1	-3.4334	1.0124	-3.3912	0.0007
1 2	-0.8736	0.9602	-0.9098	0.3629
2 3	2.,0447	0.9857	2.0743	0.0380
3 4	3.6966	1.0376	3.5628	0.0004
Attentive Condition	1.9276	0.9154	2.1057	0.0352
z.trial	0.7848	0.3017	2.6017	0.0093
z.age	-0.5619	0.5958	-0.9431	0.3456
l(z.age^2)	0.9322	0.3979	2.3429	0.0191
sexM	-0.3059	0.8374	-0.3653	0.7149

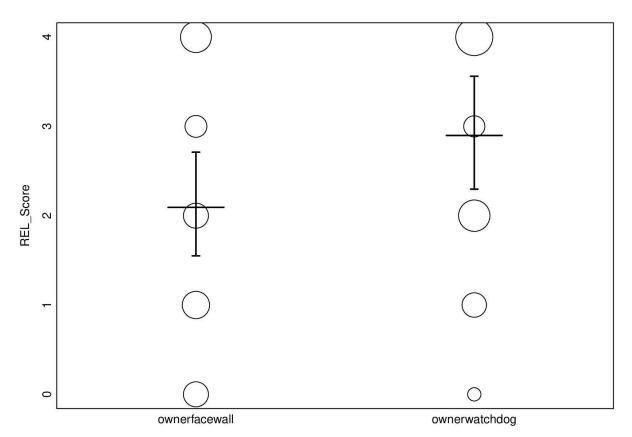


Figure 11: Relevant action copying scores depending on the caregiver attentional state, circles represent the number of individuals and lines represent the average score.

Obedience test

The mean obedience score obtained was 3 (Figure 6). Results were not analysed further as the measure was unreliable due to the behaviours varying between subjects as we attempted to score it. As such, to get a reliable measure to use in our analysis would have required significant reduction of the sample size by restricting the data to only those dogs for which the test was conducted in an identical manner. To have a valid and reliable obedience score, the test should have been implemented from the beginning of testing, after piloting, and conducted in a more standardised way.

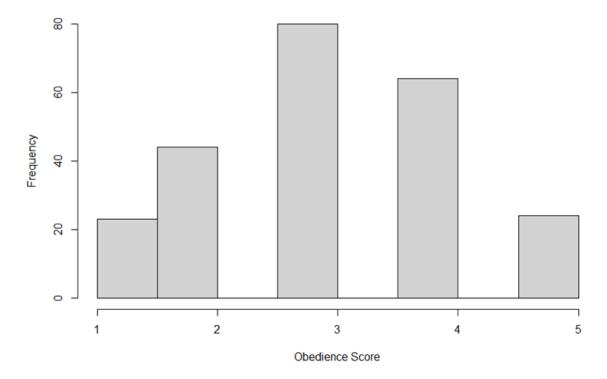


Figure 12: Histogram of the results of the obedience test.

Discussion

The results of this study, in line with previous overimitation studies (Huber et al., 2018, 2020, 2022; Mackie & Huber, 2023), support overimitation in dogs and found an effect of trial on the copying accuracy of both the relevant and irrelevant actions, but no effect of sex in the overimitative behaviour of dogs. The attentional state of the caregiver had no significant effect on the propensity of dogs to touch the goal-irrelevant dots, but had an effect on the copying accuracy of the goal-relevant action of opening the food chamber door. Surprisingly, dogs in the attentive condition, being watched by their caregiver, showed higher copying scores than those in the inattentive condition, whose caregivers had their back turned.

The statistical analysis revealed no effect of condition on the copying accuracy of the irrelevant action: the attentional state of the caregiver did not affect the dogs' propensity to overimitate. As such, the results of this study do not support obedience as the motivation behind overimitation in dogs. It is however necessary to discuss the possible link between obedience and affiliation in dogs.

In this study, we aimed to test obedience through caregiver attentional states, as these have been shown to relate to dog obedience or disobedience when food is available (Schwab & Huber, 2006; Viranyi et al., 2004), but it is possible that affiliation also played a role as attentional states might have triggered dogs' attachment, as human children overimitate less when the demonstrator is less attentive (Marsh et al., 2019; Stengelin et al., 2019). Indeed, the subjects' performance could have also derived from the opportunity to affiliate with their caregiver when they were watching versus the absence of such an opportunity when they had their back turned. Moreover, considering dogs were selected by humans to be perfect companions, it could be argued that obedience and affiliation are not as separate as they might initially appear. There is a possibility that, in pet dogs, obedience and affiliation are intrinsically linked and cannot be separated. One could argue that dogs' obedience is modulated by their affection to varying degrees, based on the dog's personality and breed for example. Dogs' willingness to obey is indeed often related to their level of affiliation to the person commanding them (Kerepesi et al., 2015). In addition to this relationship between obedience and affiliation potentially affecting the results of this study, there are also confounding factors to consider.

The first confounding factor is the previous experience of the dogs at the CDL. Dogs who are more used to participating in studies in this environment may be more confident and therefore able to behave as usual whereas inexperienced dogs' performance can be affected by their fear or curiosity in a novel environment. Since one of our study requirements was that dogs should not have previous experience of the overimitation task (at the CDL in Huber et al., 2018, 2020, 2022; Mackie and Huber, 2023), since many dogs in our database had this experience, many of my subjects were new to the CDL or at least fairly inexperienced. This could also account for the low rates of overimitation in my study compared to the previous overimitation studies conducted at the CDL. However, dogs' prior CDL experience was not initially considered in the experimental design or data analysis for this study, and therefore could not be explicitly tested for in this thesis. Future studies at the CDL may wish to consider how a dog's prior experience in CDL studies could affect their performance.

Similarly, the dogs' personality can of course affect their performance in any study and in this one in particular, as it could for example be argued that independent dogs would be less inclined to overimitate. To analyse this, however, would have required the use of a personality questionnaire, or a particular type of personality to be a criterion during subject recruitment. Another way in which personality could have influenced our results is the fact that we found that some dogs were scared of the sliding door: several dogs started opening

the door but were frightened by its movement and never opened it fully to get the reward. However, in Mackie and Huber's (2023) study, which analysed dog personality ratings, there was not any correlation between neuroticism ('fearfulness') and overimitation. Furthermore, breed and training experience are important confounding factors which probably affected our subjects' performances but that cannot be truly accounted for here, as the study would have to be designed with these factors in mind to have analysable data on these factors, which was not the case here. An important note on training experience though, is the issue of whether or not dogs were trained in finding hidden food. Indeed, this is something which should perhaps have been considered from the start and adequately managed or analysed. As it were, all caregivers were instructed to not command their dogs to search for food at the beginning of trials, but some still did whereas others didn't and argued this as the reason for their dog's lack of success. As previously mentioned, this is a criterion we did not anticipate and therefore did not plan for. Analysing this would have required to plan for groups of varying training history from the beginning or to account for training in our statistical analysis, which was not possible as we did not collect this data during testing. Including many of these extra variables would have also overcomplicated the statistical analysis, so it was decided that we would focus on obedience, age, sex, trial, and individual random effects for our analysis.

As for the relevant action copying, there was an effect of caregiver attentional state on the copying accuracy of the relevant action, with the dogs being watched by their caregivers (attentive condition) scoring higher than those whose owners were facing the wall (inattentive condition), which was unexpected. Indeed, if the dogs considered the overimitation task as a training session, we would expect, based on previous obedience research (Schwab & Huber, 2006; Viranyi et al., 2004), that they would be more reluctant to open the door and eat the food reward when being watched by their caregiver, should they believe they are not allowed to do so. But why should they do so? Quite to the contrary, the demonstration may have indicated to the dogs that they were allowed to eat the food reward. The higher score in the attentive condition could then be explained in this manner. Additionally, perhaps dogs felt more comfortable manipulating the food chamber when their caregiver was watching due to a secure base effect, in which the caregiver's presence is a reassurance for the dog, allowing it to interact more with its environment (Horn et al., 2013). This could account for increased success in the relevant action when the caregiver is more present by paying attention than when the caregiver is ignoring the dog by having their back turned. Lastly, the higher copying accuracy of dogs in the attentive condition, meaning their

increased tendency to match the door opening direction that their caregiver demonstrated, could be due to dogs considering attentive caregivers as an opportunity to affiliate, compared to inattentive caregivers. This would go in line with the hypothesis of affiliation with the caregiver being the main drive behind overimitation in dogs, but, as previously discussed, this tendency was not observed for the irrelevant action copying part of the overimitation task. This affiliative motivation to copy the goal-relevant action more than the irrelevant one could perhaps be due to dogs' strong attraction to the food reward rather than the dots. They would therefore have paid more attention to the door opening action during the demonstration, and would have been able to copy it more faithfully than the dot touching, thus showing more motivation to do so when their caregiver was paying attention.

Importantly, an overwhelming majority of dogs who overimitated did so only after obtaining the food reward by performing the relevant action. This was also observed in previous overimitation studies at the CDL (Huber et al., 2018, 2020, 2022; Mackie & Huber, 2023) and is hypothesised to be due to food being such a big motivator as well as to a recency effect, considering the door opening is the last step of the caregiver demonstration. In turn, dogs who do not manage to obtain the reward generally do not overimitate, meaning that factors which seem to only affect relevant action copying can also affect overimitation, such as fear of the door or training experience. Additionally, it could be argued that dogs do not overimitate unless they perform the irrelevant actions before the relevant action, as in most human studies. This of course depends entirely on how one defines overimitation, but it is important to remember how different the experimental designs of human and dog overimitation studies are as well as the difference between the rewards used and how motivating these are to the subjects. Moreover, there is the important difference of a conspecific or heterospecific model to consider. As such, there is sufficient evidence for overimitation in this study, but devising a new experimental design without food as a reward would give us further insight into this issue. Food may be too rewarding for dogs to the point of distraction, whereas a toy reward could be more appropriate considering it would not involve such a vital resource to dogs. This would also allow for a closer experimental design to human overimitation studies, where rewards are usually rather trivial such as stickers or marbles.

These results add more data to the larger topic of overimitation in pet dogs and especially to the question of different motivations to overimitate in comparison to humans. This study supports the hypothesis that dogs perceive overimitation as a kind of social game

in which affiliation towards the caregiver is central, whereas humans seem to view overimitation as an opportunity for normative learning or social affiliation with conspecifics.

Conclusion

To conclude, this study showed no effect of caregiver attentional state on the copying of irrelevant actions in dogs, thereby providing no support to the hypothesis that obedience motivates pet dogs to overimitate their caregivers. These results thus indirectly support affiliation as the driving force behind overimitation in companion dogs by showing that our subjects did not seem to view the overimitation task as a training session but perhaps rather a social game to play with their primary caregiver.

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References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016). Dogs recognize dog and human emotions. *Biology Letters*, *12*(1), 20150883. <u>https://doi.org/10.1098/rsbl.2015.0883</u>

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. <u>https://doi.org/10.1016/j.jml.2012.11.001</u>

Bennett, P. C., & Rohlf, V. I. (2007). Caregiver-companion dog interactions: Relationships between demographic variables, potentially problematic behaviours, training engagement and shared activities. *Applied Animal Behaviour Science*, *102*(1), 65–84. <u>https://doi.org/10.1016/j.applanim.2006.03.009</u>

Call, J., Bräuer, J., & Kaminski, J. (2003). Domestic Dogs (Canis familiaris) Are Sensitive to the Attentional State of Humans. *Journal of Comparative Psychology*, *117*(3), 257–263. <u>https://doi.org/10.1037/0735-7036.117.3.257</u>

Clark, G. I., & Boyer, W. N. (1993). The effects of dog obedience training and behavioural counselling upon the human-canine relationship. *Applied Animal Behaviour Science*, *37*(2), 147–159. <u>https://doi.org/10.1016/0168-1591(93)90107-Z</u>

Clay, Z., & Tennie, C. (2018). Is Overimitation a Uniquely Human Phenomenon? Insights From Human Children as Compared to Bonobos. *Child Development*, *89*(5), 1535–1544. <u>https://doi.org/10.1111/cdev.12857</u>

Dobson, A. J., & Barnett, A. G. (2018). *An Introduction to Generalized Linear Models* (4th ed.). Chapman and Hall/CRC. <u>https://doi.org/10.1201/9781315182780</u>

Flannigan, G., & Dodman, N. H. (2001). Risk factors and behaviors associated with separation anxiety in dogs. *Journal of the American Veterinary Medical Association*, 219(4), 460–466. <u>https://doi.org/10.2460/javma.2001.219.460</u>

Flynn, E., & Smith, K. (2012). Investigating the mechanisms of cultural acquisition: How pervasive is overimitation in adults? *Social Psychology*, *43*(4), 185–195. <u>https://doi.org/10.1027/1864-9335/a000119</u>

Fox, J., & Weisberg, S. (2019). Applied Regression 3E. In *An R Companion to Applied Regression* (Third Edition). Sage. <u>https://socialsciences.mcmaster.ca/jfox/Books/Companion/appendices.html</u>

Fukuzawa, M., Mills, D. S., & Cooper, J. J. (2005). More than just a word: Non-semantic command variables affect obedience in the domestic dog (Canis familiaris). Applied Animal Behaviour Science, 91(1), 129–141. https://doi.org/10.1016/j.applanim.2004.08.025

Gácsi, M., McGreevy, P., Kara, E., & Miklósi, A. (2009). Effects of selection for cooperation and attention in dogs | Behavioral and Brain Functions | Full Text. *Behavioral and Brain Functions*, *5*(31). <u>https://doi.org/10.1186/1744-9081-5-31</u>

Galef, B. G., & Laland, K. N. (2005). Social Learning in Animals: Empirical Studies and Theoretical Models. *BioScience*, 55(6), 489–499. <u>https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2</u>

Galibert, F., Quignon, P., Hitte, C., & André, C. (2011). Toward understanding dog evolutionary and domestication history. *Comptes Rendus Biologies*, *334*(3), 190–196. <u>https://doi.org/10.1016/j.crvi.2010.12.011</u>

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*(9), 439–444. <u>https://doi.org/10.1016/j.tics.2005.07.003</u>

Heyes, C. (2009). Evolution, development and intentional control of imitation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2293–2298. <u>https://doi.org/10.1098/rstb.2009.0049</u>

Heyes, C. M. (1994). SOCIAL LEARNING IN ANIMALS: CATEGORIES AND MECHANISMS. *Biological Reviews*, 69(2), 207–231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x

Horn, L., Huber, L., & Range, F. (2013). The Importance of the Secure Base Effect for Domestic Dogs – Evidence from a Manipulative Problem-Solving Task. *PLOS ONE*, *8*(5), e65296. <u>https://doi.org/10.1371/journal.pone.0065296</u>

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). *Animal Cognition*, *8*(3), 164–181. <u>https://doi.org/10.1007/s10071-004-0239-6</u>

Huber, L., Kubala, D., & Cimarelli, G. (2022). Overimitation in Dogs: Is There a Link to the Quality of the Relationship with the Caregiver? *Animals*, *12*(3), Article 3. <u>https://doi.org/10.3390/ani12030326</u>

Huber, L., Popovová, N., Riener, S., Salobir, K., & Cimarelli, G. (2018). Would dogs copy irrelevant actions from their human caregiver? *Learning & Behavior*, *46*(4), 387–397. <u>https://doi.org/10.3758/s13420-018-0336-z</u>

Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z., & Miklosi, A. (2009). The evolution of imitation: What do the capacities of non-human animals tell us about the

mechanisms of imitation? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2299–2309. <u>https://doi.org/10.1098/rstb.2009.0060</u>

Huber, L., Salobir, K., Mundry, R., & Cimarelli, G. (2020). Selective overimitation in dogs. *Learning & Behavior*, *48*(1), 113–123. <u>https://doi.org/10.3758/s13420-019-00400-w</u>

Jagoe, A., & Serpell, J. (1996). Caregiver characteristics and interactions and the prevalence of canine behaviour problems. *Applied Animal Behaviour Science*, *47*(1), 31–42. <u>https://doi.org/10.1016/0168-1591(95)01008-4</u>

Johnston, A. M., Holden, P. C., & Santos, L. R. (2017). Exploring the evolutionary origins of overimitation: A comparison across domesticated and non-domesticated canids. *Developmental Science*, *20*(4), e12460. <u>https://doi.org/10.1111/desc.12460</u>

Kenward, B. (2012). Over-imitating preschoolers believe unnecessary actions are normative and enforce their performance by a third party. *Journal of Experimental Child Psychology*, *112*(2), 195–207. <u>https://doi.org/10.1016/j.jecp.2012.02.006</u>

Kenward, B., Karlsson, M., & Persson, J. (2010). Over-imitation is better explained by norm learning than by distorted causal learning. *Proceedings of the Royal Society B: Biological Sciences*, 278(1709), 1239–1246. <u>https://doi.org/10.1098/rspb.2010.1399</u>

Kerepesi, A., Dóka, A., & Miklósi, Á. (2015). Dogs and their human companions: The effect of familiarity on dog–human interactions. *Behavioural Processes*, *110*, 27–36. <u>https://doi.org/10.1016/j.beproc.2014.02.005</u>

Keupp, S., Behne, T., & Rakoczy, H. (2013). Why do children overimitate? Normativity is crucial. *Journal of Experimental Child Psychology*, *116*(2), 392–406. <u>https://doi.org/10.1016/j.jecp.2013.07.002</u>

Kobelt, A. J., Hemsworth, P. H., Barnett, J. L., & Coleman, G. J. (2003). A survey of dog caregivership in suburban Australia—Conditions and behaviour problems. *Applied Animal Behaviour Science*, *82*(2), 137–148. <u>https://doi.org/10.1016/S0168-1591(03)00062-5</u>

Legare, C. H., & Nielsen, M. (2015). Imitation and Innovation: The Dual Engines of Cultural Learning. *Trends in Cognitive Sciences*, *19*(11), 688–699. <u>https://doi.org/10.1016/j.tics.2015.08.005</u>

Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences*, *104*(50). <u>https://doi.org/10.1073/pnas.0704452104</u>

Mackie, L., & Huber, L. (2023). Socially priming dogs in an overimitation task. *Frontiers in Psychology*, *14*, 1063132. <u>https://doi.org/10.3389/fpsyg.2023.1063132</u>

Marsh, L. E., Ropar, D., & Hamilton, A. F. de C. (2019). Are you watching me? The role of audience and object novelty in overimitation. *Journal of Experimental Child Psychology*, *180*, 123–130. <u>https://doi.org/10.1016/j.jecp.2018.12.010</u>

Marshall-Pescini, S., Frazzi, C., & Valsecchi, P. (2016). The effect of training and breed group on problem-solving behaviours in dogs. *Animal Cognition*, *19*(3), 571–579. <u>https://doi.org/10.1007/s10071-016-0960-y</u>

Marshall-Pescini, S., Passalacqua, C., Barnard, S., Valsecchi, P., & Prato-Previde, E. (2009). Agility and search and rescue training differently affects pet dogs' behaviour in socio-cognitive tasks. *Behavioural Processes*, *81*(3), 416–422. <u>https://doi.org/10.1016/j.beproc.2009.03.015</u>

Marshall-Pescini, S., Valsecchi, P., Petak, I., Accorsi, P. A., & Previde, E. P. (2008). Does training make you smarter? The effects of training on dogs' performance (Canis familiaris) in a problem solving task. *Behavioural Processes*, *78*(3), 449–454. <u>https://doi.org/10.1016/j.beproc.2008.02.022</u>

McGuigan, N., Makinson, J., & Whiten, A. (2011). From over-imitation to super-copying: Adults imitate causally irrelevant aspects of tool use with higher fidelity than young children. *British Journal of Psychology*, *102*(1), 1–18. <u>https://doi.org/10.1348/000712610X493115</u>

McGuigan, N., & Whiten, A. (2009). Emulation and "overemulation" in the social learning of causally opaque versus causally transparent tool use by 23- and 30-month-olds. *Journal of Experimental Child Psychology*, *104*(4), 367–381. https://doi.org/10.1016/j.jecp.2009.07.001

McGuigan, N., Whiten, A., Flynn, E., & Horner, V. (2007). Imitation of causally opaque versus causally transparent tool use by 3- and 5-year-old children. *Cognitive Development*, *22*(3), 353–364. <u>https://doi.org/10.1016/j.cogdev.2007.01.001</u>

Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., Blackwell, E., & Casey, R. (2010). Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. *Current Biology*, *20*(19), R839–R840. <u>https://doi.org/10.1016/j.cub.2010.08.030</u>

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A Simple Reason for a Big Difference: Wolves Do Not Look Back at Humans, but Dogs Do. *Current Biology*, *13*(9), 763–766. <u>https://doi.org/10.1016/S0960-9822(03)00263-X</u>

Miklósi, Á., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, *1*(2), 113–121. <u>https://doi.org/10.1007/s100710050016</u>

Müller, C. A., Schmitt, K., Barber, A. L. A., & Huber, L. (2015). Dogs Can Discriminate Emotional Expressions of Human Faces. *Current Biology*, *25*(5), 601–605. <u>https://doi.org/10.1016/j.cub.2014.12.055</u>

Nielsen, M. (2012). Imitation, pretend play, and childhood: Essential elements in the evolution of human culture? *Journal of Comparative Psychology*, *126*(2), 170–181. <u>https://doi.org/10.1037/a0025168</u>

Nielsen, M., & Blank, C. (2011). Imitation in young children: When who gets copied is more important than what gets copied. *Developmental Psychology*, *47*(4), 1050–1053. <u>https://doi.org/10.1037/a0023866</u>

Nielsen, M., Mushin, I., Tomaselli, K., & Whiten, A. (2014). Where Culture Takes Hold: 'Overimitation' and Its Flexible Deployment in Western, Aboriginal, and Bushmen Children on JSTOR. *Child Development*, *85*(6), 2169–2184. <u>http://www.jstor.org/stable/24696721.</u>

Nielsen, M., Simcock, G., & Jenkins, L. (2008). The effect of social engagement on 24-month-olds' imitation from live and televised models. *Developmental Science*, *11*(5), 722–731. <u>https://doi.org/10.1111/j.1467-7687.2008.00722.x</u>

Nielsen, M., & Susianto, E. W. E. (2011). Failure to find over-imitation in captive orangutans (Pongo Pygmaeus): Implications for our understanding of cross-generation information transfer. *Developmental Psychology*, 153–168.

Nielsen, M., & Tomaselli, K. (2010). Overimitation in Kalahari Bushman Children and the Origins of Human Cultural Cognition. *Psychological Science*, *21*(5). <u>https://doi.org/10.1177/0956797610368808</u>

Nieuwenhuis, R., Grotenhuis, M. te, & Pelzer, B. (2012). influence.ME: Tools for Detecting Influential Data in Mixed Effects Models. *The R Journal*, *4*(2), 38–47. <u>https://journal.r-project.org/archive/2012/RJ-2012-011/index.html</u>

Over, H., & Carpenter, M. (2012). Putting the social into social learning: Explaining both selectivity and fidelity in children's copying behavior. *Journal of Comparative Psychology*, *126*(2), 182–192. <u>https://doi.org/10.1037/a0024555</u>

R Core Team. (2022). *R: The R Project for Statistical Computing*. <u>https://www.r-project.org/</u>

Range, F., Viranyi, Z., & Huber, L. (2007). Selective Imitation in Domestic Dogs. *Current Biology*, *17*(10), 868–872. <u>https://doi.org/10.1016/j.cub.2007.04.026</u> Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. <u>https://doi.org/10.1111/j.2041-210X.2010.00012.x</u>

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. <u>https://doi.org/10.1093/beheco/arn145</u>

Schwab, C., & Huber, L. (2006). Obey or not obey? Dogs (Canis familiaris) behave differently in response to attentional states of their caregivers. *Journal of Comparative Psychology (Washington, D.C.:* 1983), 120(3), 169–175. https://doi.org/10.1037/0735-7036.120.3.169

Sherman, B. (2008). Separation anxiety in dogs. *Compendium on Continuing Education for the Practising Veterinarian -North American Edition-*. 30. 27-42. https://www.researchgate.net/publication/5572881_Separation_anxiety_in_dogs

Soproni, K., Miklósi, A., Topál, J., & Csányi, V. (2001). Comprehension of human communicative signs in pet dogs (Canis familiaris). *Journal of Comparative Psychology*, *115*(2), 122–126. <u>https://doi.org/10.1037/0735-7036.115.2.122</u>

Stengelin, R., Hepach, R., & Haun, D. B. M. (2019). Being observed increases overimitation in three diverse cultures. *Developmental Psychology*, *55*(12), 2630–2636. <u>https://doi.org/10.1037/dev0000832</u>

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 364(1528), 2405–2415. <u>https://doi.org/10.1098/rstb.2009.0052</u>

Topál, J., Byrne, R. W., Miklósi, A., & Csányi, V. (2006). Reproducing human actions and action sequences: 'Do as I Do!' in a dog. *Animal Cognition*, *9*(4), 355–367. <u>https://doi.org/10.1007/s10071-006-0051-6</u>

Van Schaik, C. P. (2010). Social learning and culture in animals. In P. Kappeler (Ed.), *Animal Behaviour: Evolution and Mechanisms* (pp. 623–653). https://doi.org/10.1007/978-3-642-02624-9_20

Vas, J., Topál, J., Gácsi, M., Miklósi, A., & Csányi, V. (2005). A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Applied Animal Behaviour Science*, *94*(1–2), 99–115. <u>https://doi.org/10.1016/j.applanim.2005.02.001</u> Virányi, Z., Topál, J., Gácsi, M., Miklósi, Á., & Csányi, V. (2004). Dogs respond appropriately to cues of humans' attentional focus. *Behavioural Processes*, *66*(2), 161–172. <u>https://doi.org/10.1016/j.beproc.2004.01.012</u>

Vivanti, G., Hocking, D. R., Fanning, P., & Dissanayake, C. (2017). The social nature of overimitation: Insights from Autism and Williams syndrome. *Cognition*, *161*, 10–18. <u>https://doi.org/10.1016/j.cognition.2017.01.008</u>

Voith, V. L., Wright, J. C., & Danneman, P. J. (1992). Is there a relationship between canine behavior problems and spoiling activities, anthropomorphism, and obedience training? *Applied Animal Behaviour Science*, *34*(3), 263–272. <u>https://doi.org/10.1016/S0168-1591(05)80121-2</u>

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682–685. <u>https://doi.org/10.1038/21415</u>

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2417–2428. <u>https://doi.org/10.1098/rstb.2009.0069</u>

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Supplementary Materials

<u>S1</u>: List of all dog subjects, detailing their name, age, sex, breed and condition

Name	Age	Breed	Sex	Condition
Jamie7	4	Greyhound	М	ownerfacewall
Nox3	8	Mix	М	ownerfacewall
Amarie	10	Mix	F	ownerwatchdog
Anthony	9	English Setter	М	ownerfacewall
Ambiano	5	Picardy Spaniel	М	ownerwatchdog
Milo7	3	Australian Shepherd	М	ownerwatchdog
Boo2	9	Mix	F	ownerwatchdog
Trixi2	8	Schnauzer	F	ownerwatchdog
Yuki7	3	Mix	F	ownerwatchdog
Choki	2	Mix	М	ownerfacewall
Jack7	1	Australian Shepherd	М	ownerfacewall
Nikita4	4	Australian Shepherd	F	ownerwatchdog
Maze	1	Mix	F	ownerfacewall
Ava2	6	Louisiana Catahoula Leopard Dog	F	ownerwatchdog
Pisco	1	Parson Jack Russell Terrier	М	ownerfacewall
Skadi3	1	Australian Shepherd	F	ownerfacewall

Loki6	7	Great Swiss Mountain Dog	М	ownerwatchdog
Loomis	2	Golden Retriever	М	ownerwatchdog
Riley	12	Border Collie	F	ownerwatchdog
Dazzle	1	Border Collie	F	ownerfacewall
Siri	6	Border Collie	F	ownerfacewall
Jack	12	Border Collie	М	ownerwatchdog
Diego6	5	Border Terrier	М	ownerwatchdog
Lucy18	1	Miniature Poodle	F	ownerfacewall
Kalea	2	Labrador Retriever	F	ownerfacewall
Lexi3	3	Mix	F	ownerfacewall
Akido	8	Mix	М	ownerwatchdog
Goofy2	1	Mix	М	ownerwatchdog
Chewie	4	Bernese Mountain Dog	М	ownerwatchdog
Toffee5	3	Bernese Mountain Dog	F	ownerfacewall
Hero	1	Whippet	М	ownerwatchdog
Bingo	6	Mix	М	ownerwatchdog
Michi	3	Rhodesian Ridgeback	М	ownerfacewall
Mazekeen	4	Kleiner Münsterländer	F	ownerwatchdog
Loki7	1	Mix	М	ownerfacewall

Ylvie	3	Deutscher Pinsher	F	ownerwatchdog
Arthur3	8	Rhodesian Ridgeback	М	ownerwatchdog
Caruso2	1	Mix	М	ownerfacewall
Butch	3	Boxer	М	ownerwatchdog
Ferdinand	6	Mix	М	ownerfacewall
Eben	3	Mix	F	ownerwatchdog
Gandalf	3	Andalusian Hound	М	ownerwatchdog
Nala15	1	Mix	F	ownerfacewall
Diara	2	Rhodesian Ridgeback	F	ownerwatchdog
Fanny9	3	Standard Poodle	F	ownerwatchdog
Elly2	2	Mix	F	ownerfacewall
Daisy5	2	Golden Retriever	F	ownerwatchdog
Anubis3	4	Italian Greyhound	М	ownerfacewall
Nala13	2	Mix	F	ownerwatchdog
Tyson	5	Mix	М	ownerwatchdog
Nala16	1	Golden Retriever	F	ownerfacewall
Resi2	1	Magyar Vizsla	F	ownerfacewall
Flee	4	Siberian Husky	М	ownerwatchdog
Yuki5	5	Siberian Husky	F	ownerfacewall

Levi2	4	Mix	М	ownerfacewall
Tofu	1	Cocker Spaniel	М	ownerfacewall
Bud	4	Welsh Corgi Pembroke	М	ownerwatchdog
Terence	4	Welsh Corgi Pembroke	М	ownerfacewall
Teodor	4	Mix	М	ownerfacewall
Lina3	7	Mix	F	ownerwatchdog
Lola8	2	Mix	F	ownerfacewall
Ella3	1	Mix	F	ownerwatchdog
Raya	1	Mix	F	ownerfacewall